SEXUAL HARASSMENT AMONG FEMALE LION-TAILED MACAQUES (*MACACA SILENUS*) IN THE WILD[1]

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(*With three text-figures*)

Key words: reproductive suppression, sexual swelling, *Macaca silenus*, mounting frequency

Adult female lion-tailed macaques often harass sexually interacting adult male and female members of the group. The extent of harassment and its implication for reproduction by females was studied in a group in the Anaimalai (presently Indira Gandhi) Wildlife Sanctuary, Tamil Nadu, India. Nearly 1560 hours of observation were made on the same group during nine months in 1979-80 and 15 months in 1982-84. A total of 577 sexual interactions between single adult male and females were recorded. Most of the sexual mountings occurred when the females had sexual swelling with a peak 2-4 days prior to deflation of the swelling. Most of the harassment was by females with sexual swelling. Harassment decreased the probability of mating taking place once a sexual interaction had been initiated (from 0.582 to 0.07). Aggressive harassment significantly reduced the duration of mating (from 9.12 secs to 6.16 secs), and thus probably prevented ejaculation. The percentage of sexual interactions that were harassed increased with the number of females with sexual swelling. Postponement of conception due to harassment might be a major reason for the absence of a synchrony in conceptions and births similar to that seen in sexual swelling soon after the summer amenorrhea. Sexual harassment is unlikely to serve as a behavioural means of population regulation. This is because fewer females show sexual swelling as the group becomes larger, probably due to increasing competition for food resources. The major reason for the occurrence of sexual harassment in the lion-tailed macaque might be competition among females for mating. This competition results from a high synchrony in sexual swelling among the females, the tendency for groups to have only one adult male, a high female to male (5:1) ratio, and multiple mount pattern in the male.

INTRODUCTION

Reproductive suppression of ovulating females occurs in some primates. In *Theropithecus gelada,* females actively disrupt each other's copulation (Mori, 1979). In the same species anovulatory cycles and premature termination of menstrual cycles and implantation occur in low ranking females from social stress due to harassment by high ranking females (Dunbar, 1980). Reproductive suppression from social stress also occurs in *Papio cynocephalus* (Wasser, 1983). In captivity, female rhesus monkeys could be prevented from mating by aggression from high ranking females (Keverne, 1983). Reproductive suppression of ovulating females has also been demonstrated in captive *Miopithecus talapoin* (Abbot *et al.*, 1986). In marmoset monkeys (*Callithrix jacchus*) ovulation by subordinate females is physiologically suppressed by the mere presence of the dominant females (Abbot, 1988).

Lion-tailed macaque, confined to the rain forests of the Western Ghats of South India, mostly live in one male units with a mean group size of 18-20 animals (Kumar, 1995a). The reproductive biology is characterized by a high sex ratio in favour of females (1:5), a conspicuous sexual swelling phase to which compulatory mountings are mostly confined, and a low birth rate (0.30/female year) compared to other macaques (Kumar 1987, 1995a). There is also a

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high degree of synchrony in the incidence of sexual swelling among the females. Harassment of the mating pair by others, especially by adult females, is frequent. This study examines the extent of harassment of matings pairs and its implication for reproduction by the females. Whether such harassment could play a population regulatory role is also discussed, since birth rate has been found to decrease with increasing group size (Kumar, 1995b).

METHODS

The analysis is based primarily on data collected during an ecological study on one group in the Anaimalai (presently Indira Gandhi) Wildlife Sanctuary, Tamil Nadu State, from March 1979 to March 1980, and from December 1982 to March 1984. The group was located in Varagaliyar shola, about 25 km south of Top Slip, the Sanctuary headquarters. Varagaliyar shola is about 20 sq. km in area and is the largest of the rain forest fragments in the Sanctuary. This shola had five or six groups of lion-tailed macaque. The main study group had only one adult male during both the study periods. There was no subadult male in 1979-80, and one in 1982-84. The number of adult females varied from 5 in 1979-80 to 9 in 1982-84 (Table 1).

TABLE 1
COMPOSITION OF THE MAIN STUDY GROUP IN THE INDIRA GANDHI WILDLIFE SANCTUARY IN 1979-80 AND 1982-84

Year	Adult males	Subadult males	Adult females	Immatures	Total
Jan 1979	1	0	5	6	12
Mar 1980	1	0	5	9	15
Dec 1982	1	1	6	9	17
Mar 1984	1	1	9	12	23

Data on the incidence and duration of sexual cycles come from records on the sexual status (presence or absence of swelling) of females in the study group. These records were made during five to eight days of dawn to dusk observation of the group every month, and at least once in a week during the remaining part of the month. All sexual interactions between the adult male and females were recorded *ad libitum* during dawn to dusk observation, along with the sexual status of the female. The copulatory calls of the females (see below), given during more than 80% of the sexual mounting and audible up to 75 m, was used as an indicator of mounting. Mounting frequency/hour was estimated for each day by dividing the number of mountings (seen and heard) by the number of hours of observation. Only days with dawn to dusk observation were selected for analyses, since mounting showed a strong diurnal variation. Five to eight days of such observations were carried out each month between March 1979 and January 1980 (except for July and August when no data was collected) and again between December 1982 and February 1984 (except for January and February 1984 when only two days of observations were done each month). A total of 631 hours of *ad libitum* records were made in nine months in 1979-80 and 937 hours in 15 months in 1982-84. Besides the study group, six other groups were monitored at intervals of 30-40 days in 1979-80 and 1982-84. Data on seasonality of births were taken from these groups (see Kumar, 1987).

RESULTS

Female Sexual Cycle: The female sexual cycle in the lion-tailed macaque is characterized by the cyclical appearance of sexual swelling in the perineal region and at the base of the tail which is conspicuous (Fooden, 1975). The swelling phase had a mean length of 14.1 days (range 8-19 days, n=7) and the non-swelling phase had a mean length of 16.4 days (range 6-25, n=7). The combined duration of these phases gave a mean cycle length of 30.5 days. More than 80% of the mountings by the adult male occurred

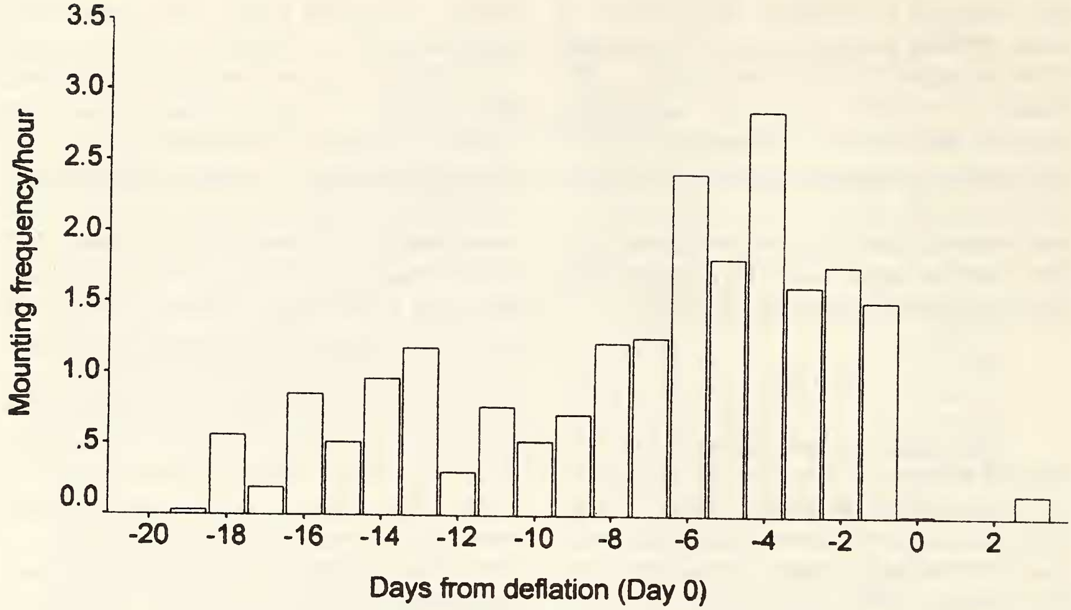

Fig. 1: Mounting frequency (per hour) by the adult male on successive days of a sexual swelling cycle of a female: mean for six sexual cycles. The sexual cycles were aligned by the day on which the swellings disappeared (day 0).

when the female had sexual swelling. Nearly 84% of these mountings were accompanied by copulatory calls of the females, compared to only 9.1% in the case of females without swelling (χ^2 = 24.9, df=1, p<0.001). The mounting frequency started to increase 3 to 4 days before the appearance of the swelling and reached a peak (of about 3/hour) four days prior to its disappearance. It then dropped abruptly almost to zero on the last day of swelling (Fig. 1). The interval between the appearance of the swelling and peak sexual activity varied from 10 to 15 days, with a mean of 12.2 days (n=6).

When data from 1979-80 and 1982-84 were combined, swellings were seen in the study group in all months of the year except March and April. In May, swelling was seen only in the last week in 1979 and none in 1983 (Fig. 2). Although there are no systematic data from the other groups, no swellings were seen in them during March-May of 1979 and 1983. It appears, therefore, that there is a summer amenorrhea in the lion-tailed macaque in the months of March and April, probably extending to May. There was a synchrony of sexual cycles in the study group soon after the first cycle following the summer amenorrhea (Fig. 2). In 1979, the sexual cycle of two females started in the last week of May, and in June all the five females of the group had sexual cycles. The sexual cycle of two subadult females started only in September-October. All the four adult females which showed swelling in 1982-83 did so in synchrony in October 1983, one sexual cycle after the first cycle of the season. (Four of the remaining five females were in post-partum amenorrhea. The fifth, the oldest female of the group, did not show swelling in 1982-84). The cycle of the subadult female started only one month later.

Sexual Harassment: Sexual harassment consisted of activities by members of the group that apparently interfered with sexual

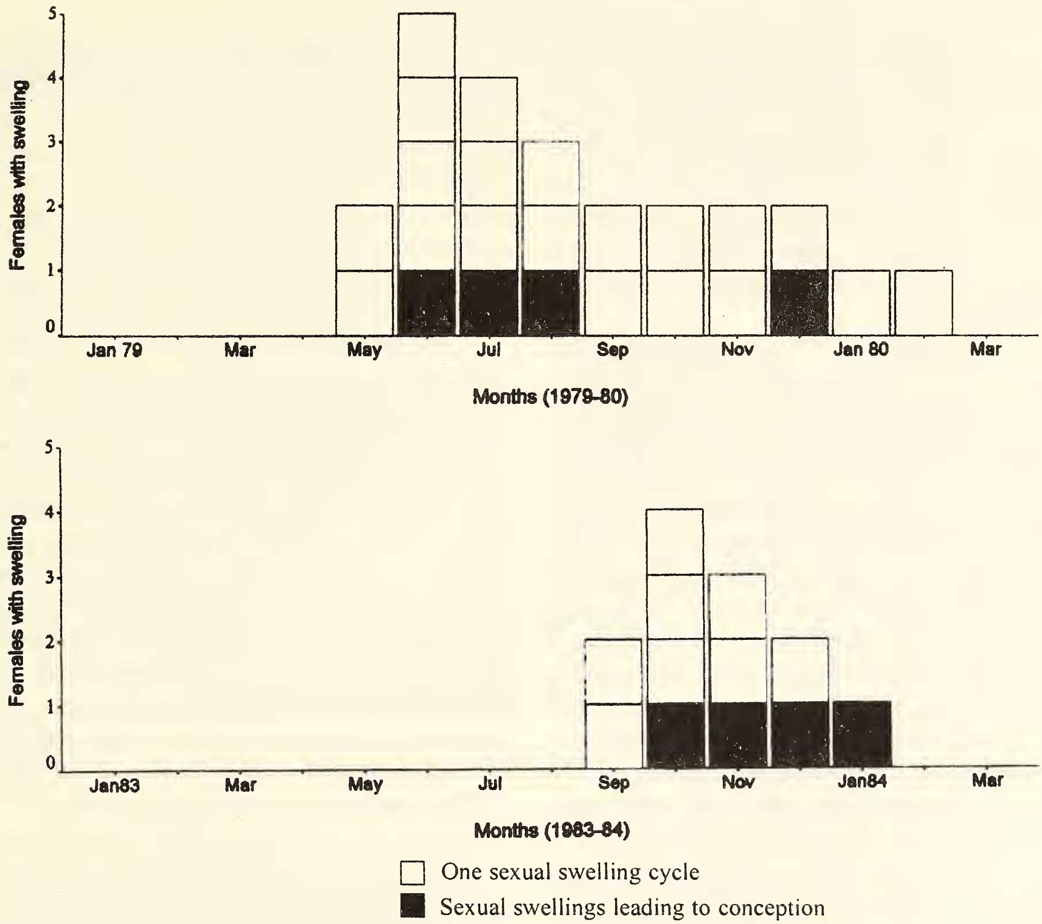

Fig. 2: The distribution of sexual cycles and conceptions in the adult females of the study group in 1970-80 and 1982-84.

interactions between adult male and female. Such interference occurred in 12.8% of the 577 sexual interactions observed. Interference occurred at the premounting stage (i.e. after the initiation of sexual interaction but before mounting) or at the mounting stage. Most of the interference were at the latter stage (70.3%).

Out of 74 harassments recorded, 23.0% were by infants and juveniles. These occurred mostly at the mounting stage, and consisted of rushing to the mating pair, and then moving about rapidly in short arcs about 2-3 m away (with tail-wagging and uttering '*uh uh*' sounds) until the mounting was over. Mountings involving females with and without sexual swellings were equally harassed by the immatures (Fisher exact test p=0.33). Moreover, mounting did not appear to discontinue as a result of such harassment.

Harassment by the subadult and adult females was related to the sexual status of the female interacting with the male. In 1982-84. 11.9% of the 270 sexual interactions involving females with swelling were harassed by other adult females, while none of the 69 mountings involving females without swelling were harassed (χ^2=7.7, df=1, p<0.01). In 1979-80, 13.1% of the 145 sexual interactions involving females with swelling were harassed by other adult females as opposed to only 2.2% of 90 sexual interactions involving female without sexual swelling (χ^2=6.8, df=1, p<0.01). About 5.2% of the sexual interactions were harassed by the subadult and adult females at the pre-mounting stage and a further 12.1% at the mounting stage.

Harassment at the pre-mounting stage consisted of a female presenting to the adult male while another female was presenting, often between the male and the first female. Sometimes a female rushed to a presenting female with aggressive calls and chased it away from the male or physically prevented the male from mounting by pulling it by the tail or by standing in the way. Harassment at the premounting stage occasionally resulted in the redirection of mounting to the harasser (21.4%). More often it prevented mounting from taking place. The percentage of sexual initiations which ended in mounting when harassed by adult females (7.0%) was significantly lower than those which were not harassed (58.2%, χ^2=12.0, df=1, p<0.001).

Harassment at the mounting stage consisted of rushing to the pair with growls, and chasing and often physically attacking the female. Presenting in front of the mounted pair was also seen. Mounting of the harasser soon after mounting the harassed female occurred in 11.1% of the cases. When harassment was overtly aggressive the harassed female often ran or jumped away before the male had dismounted. Significantly fewer of the harassed mountings were accompanied by copulatory calls (63.3%) than those which were not harassed (83.6%, χ^2=4.6, df=1, p<0.05). Harassed mountings had a shorter duration (mean=7.75 secs, s.e=0.89, n=12), than normal mountings (mean=9.12 secs, s.e=0.35, n=95). However, duration of only those which were aggressively harassed (mean=6.16 secs. s.e=0.72, n=9) was significantly shorter (t-test, t=2.6, p<0.05).

In short, harassment (a) was mostly by adult females with sexual swelling; (b) was targeted at females with sexual swelling (c) drastically decreased the probability of mounting taking place after the initiations of a sexual interaction, from 0.582 to 0.07; (d) caused a premature termination of mounting and thus probably prevented ejaculation; and (e) redirected mounting from the harassed to the harasser.

Harassment and Synchrony in Sexual Swelling: The frequency of harassment varied with the number of females with swelling. At the pre-mounting stage, 1.3% of the sexual interactions were harassed with two females with swelling and 13.7% with four such females (χ^2=14.5, df=3, p<0.001, Table 2). Harassment at the mounting stage also increased with the number of females with swelling in the group, although the difference was not significant (χ^2=5.09, df=3, p>0.10). Harassment at the mounting stage was significantly more frequent when there were three females with swelling (33.3%) compared to when there was only one (7.3%, Fisher exact test, p=0.04).

TABLE 2
PERCENTAGE OF SEXUAL INTERACTIONS, HARASSED AT THE PREMOUNTING AND MOUNTING STAGES BY ADULT FEMALES, AND ESTIMATED PERCENTAGE OF MATING CURTAILED

Number of females with swelling	Sexual interactions seen	% harassed premount mount stage	% harassed mounting stage
0	69	0	0
1	108	1.9	7.3
2	75	1.3	14.3
3	14	7.1	33.3
4	73	13.7	11.6

The frequency of mounting by the male showed significant differences between days, depending on the number of females with swelling. (Kruskal-Wallis one-way analysis of variance (K-W test), χ^2=13.4, p<0.005, Table 3). However, it did not increase in proportion to the

Table 3
MOUNTING FREQUENCY (PER HOUR) BY THE ADULT MALE AND SUBADULT MALE WHEN THERE WERE 0 TO 4 FEMALES WITHSEXUAL SWELLING IN THE GROUP

		Number of females with swelling				
		0	1	2	3	4
Adult male	Mean	0.09	0.42	1.66	1.37	**1.53**
	Min.	0.00	0.00	1.14	0.27	1.24
	Max.	2.50	1.24	2.53	2.45	1.90
Subadult	Mean	0.04	0.04	0.23	0.30	**0.22**
Male	Min.	0.00	0.00	0.00	0.00	0.00
	Max.	1.50	0.10	0.38	0.82	0.36

number of females with swelling, but appeared to reach a plateau when there were two females with swelling. The single subadult male in the group in 1982-84 had a mating frequency that was considerably lower than that of the adult male, but seemed to increase as the number of females with swelling increased (Table 3). However, the duration of mounting was considerably shorter for the subadult male (often less than 5 secs), and also did not show the characteristic multiple mount pattern of the adult male.

Consequences of Harassment: If harassment significantly reduces the frequency of ejaculatory mating, this could result in a reduction in the chances of conception by female. This is particularly so if harassment is asymmetrically distributed among the females, for example due to social dominance. Dominance interactions were relatively few and occurred mainly on major feeding trees when visibility was poor. As a result, the dominance hierarchy of females in the main study group was not precisely known. Moreover, it was often impossible to identify the females because of the speed with which harassments occurred and poor visibility. Therefore, the reproductive consequences of harassment was examined indirectly. The distribution of conceptions and births in the study group was used to test whether females were less likely conceive when there were more than one female with swelling. If this is so, then conceptions and births would not show a synchrony similar to that shown by sexual swelling, but would be more evenly spread out across the months.

The date of births in the group during the study period were known. For these, the months of conception were estimated using a gestation period of 172 days (Lindburg and Lasley, 1985). Conceptions did not have a peak corresponding to that of sexual swelling at the beginning of the season (Fig. 1). Of the five females which had swellings in June 1979, only one conceived during that month. There were no data on sexual cycles in July and August, but only one each of four remaining females conceived in July and August. The cycles of the remaining two females continued in synchrony until one conceived in December. Since the second study ended before the births from the 1983-84 mating season (September 1983 to February 1984), stoppage of cycling by females was taken as indicating conception. Two females which showed swelling in September 1983 did so again in October, when the four females which showed sexual swelling during that mating season, did so in synchrony. The cycle of only one stopped after that month. The remaining three females showed swelling in November (along with a subadult female), but only two conceptions occurred. The cycle of the remaining adult female continued until December 1983. The subadult female's cycle continued until the end of the field study in February 1984.

Population regulation: Sexual harassment could potentially play a population regulatory role since the number of females that postpone conception, especially to the next reproductive year, could increase with group size. If this is the case, then the births in the larger groups should be more dispersed among the months. This was tested with data on births from the main study group and six other groups that were periodically monitored. The seven groups were divided into two group size classes (12-18 and

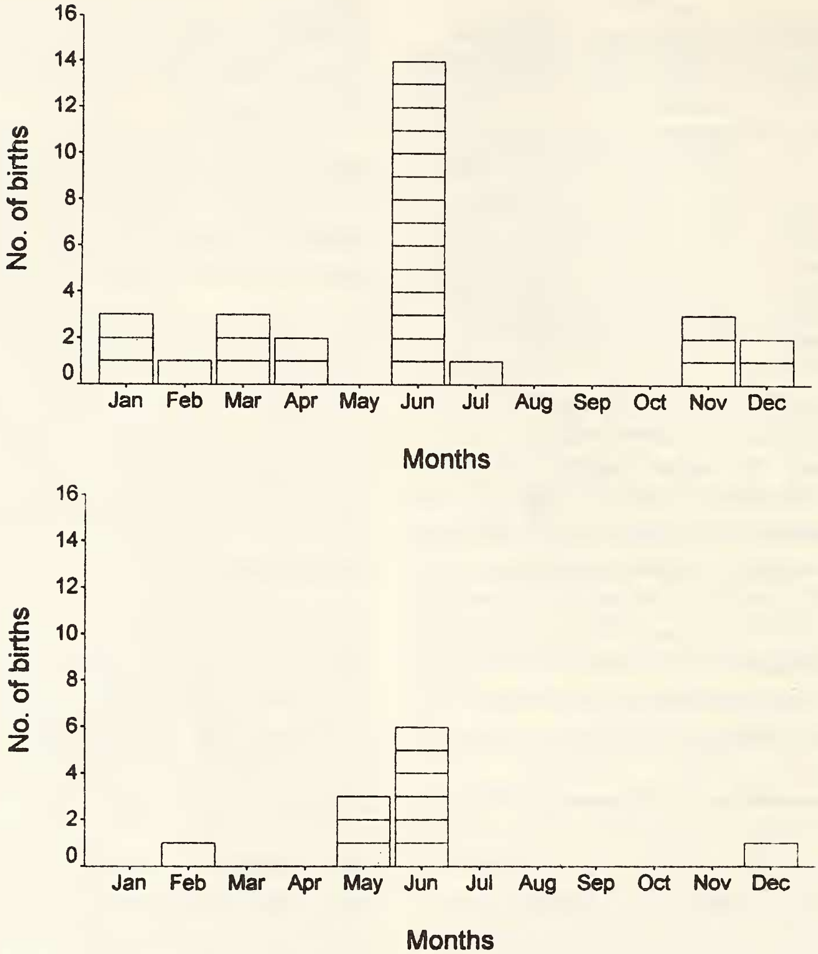

Fig. 3: The distribution of births in two group-size classes, 12-18 (above) and 19-28 (below). Each square represents one birth.

19-28) based on the mean group size during the study period (Fig. 3). Both the classes had the same mean birth date (Caughley 1977), June 15, but the coefficient of variation for the smaller class (205.0%) was nearly twice that of the larger class (112.2%). Thus, contrary to what was expected, births in the smaller groups were more dispersed through the year than the larger groups. It is also noteworthy that the main study group had a shorter mating season in 1983-84 when the group size was 17, compared to that in 1979-80 when the group size was 12 (Fig. 2).

Discussion

Sexual harassment by adult females probably occurs as a consequence of the high synchrony of sexual swelling among the females of a group, a high female/male ratio (5:1), and the tendency for the groups to be one-male units. These could lead to considerable sexual competition among the females. The multiple-mounting pattern of the male (Fooden, 1975; Kumar and Kurup, 1985) might also impose constraints on the mating potential of the male.

This competition could increase with the number of females in sexual synchrony. The extent to which harassment could affect the probability of conception would depend on the stage of the sexual cycle in relation to ovulation and the degree of asymmetry in the direction of harassment. Even though the frequency of mounting in the first week of swelling was highly variable even when there was only one sexually active female (Kumar, 1987), the peak between 2-5 days prior to deflation indicates that mountings at this stage of the cycle might be critical to conception. Thus, harassment in the last week of swelling could severely affect the probability of conception. At extreme asymmetry, in the direction of harassment, all the curtailed mountings could be of the low-ranking females. In addition, if harassments between females of different ranks differed in aggressiveness (for example, those by dominant females being more aggressive) mounting by the low-ranking females could be curtailed more than those of dominant females since aggressive harassments were more effective in curtailing mounting.

Birth rate in the lion-tailed macaques is a decreasing function of group size and the number of adult females in the group (Kumar, 1995b). Sexual harassment could lead to such an effect and thus serve as a population regulatory factor, if two conditions are met: i) the proportion of females coming into sexual synchrony during the mating season should be constant with group size, so that their absolute number would increase with group size; and ii) groups should be either one male units irrespective of group size, or when there is more than one male, only one of them is reproductively active during all the phases of the sexual cycle of the females. If these conditions are met, then the mating season should be more prolonged with increasing group size, as more females postpone conception. Therefore, births should be more dispersed in the larger groups and have a higher coefficient of variation. The limited data on the main study group shows that the mating season gets shorter, and not longer as predicted, as the group becomes larger. Also, contrary to the second prediction, births were relatively less dispersed in the larger groups than in the smaller groups. This was probably because of the violation of the above two conditions.

It is known that females do not ovulate until they reach a particular nutritional level (Frisch and McArthur 1974). Since resource competition increases with group size, it could be expected that the number of females able to build up sufficient nutritional reserves, so as to start ovulation, would decrease with increasing group size. There is no systematic data on the number of females coming into sexual cycle as a function of group size. In one large group with more than 25 members, which was regularly censused, not more than 4 of the 12 females were ever seen with sexual swelling on the same day. Since births in the larger groups were few, it was unlikely that other females were in post-partum amenorrhea. Moreover, although the group was seen almost every month in 1979, swellings were seen only in June and November-December (with 2 and 3-4 females respectively).

In addition, the number of adult and subadult males increase with group size (Kumar, 1987). No data was collected on the sexual behaviour of males in multi-male groups. The limited data on sexual behaviour of the subadult male of the study group indicate that mounting frequency of subadult males increased with the number of sexually active females in the group (Table 3). Even if mountings by the subadult male (and probably low ranking adult males of multi-male groups) are confined to the early follicular and luteal phases of the cycle, such mountings could significantly reduce the sexual competition between the females with overlapping sexual cycles. As a result, mountings by the adult male (or dominant male in multi-male groups), even if only confined to the late follicular phase, could be less harassed by other females which are in other phases of the cycle.

The short birth season in the larger groups might be, therefore, a cumulative function of (a) fewer females coming into sexual cycles in each season which in itself would significantly reduce female sexual competition and (b) more adult males in the larger groups which would further reduce female sexual competition. Thus, it appears unlikely that sexual harassment could be a population regulatory factor, in the small and large groups. In the former, in spite of female sexual competition (resulting from one male and several sexually active females), postponement of conception is expected to be only within the mating season. In the larger groups, on the other hand, fewer females ovulate in the mating season. It is possible that ovulating females are still sufficiently numerous in the medium sized one male groups, so that sexual competition could be high. A few females would be forced to postpone conception to the next mating season thus leading to/reproductive suppression.

Postponement of conception within the season could serve indirectly as a population regulatory factor. Increased mortality of infants born in late season has been reported; for example in *M. mulatta* (Drickammer, 1974) and in *A. palliatta* (Froelich *et al.*, 1981). Since postponement of conception is expected to increase with group size within the small to medium-size range, late season births and infant mortality could be expected to increase with group size within that range.

Acknowledgements

I am grateful to Tamil Nadu Forest Department for facilities provided in the field; to Zoological Survey of India for funding in 1977-80, to Wenner-Gren Foundation, L.S.B. Leaky Foundations, WWF-US, WWF-India, and Cambridge Commonwealth Trust for grants in 1981-87; and to Wildlife Conservation Society, New York, for grants in 1987-89. Earlier drafts of this paper greatly benefited from comments by Drs. D.J. Chivers, E.L. Bennet, J.M.Y. Robertson, E. Barret, L. Fuller, E.B. Keverne, and G.W. Norton.

References

Abbott, D.H. (1988): Social suppression of reproduction in primates. *In*: Comparative Socioecology: The Behavioural Ecology and Humans and Other Animals (Eds. V. Standen and R.A. Foely), pp. 285-304.

Abbot, D.H., E.B. Keverne, G.F. Moore & U. Yodyingyard (1986): Social suppression of reproduction in subordinate talapoin monkeys, *Miopithecus talapoin*. *In*: Primate Ontogeny, Cognition and Reproductive Behaviour (Eds. J.G. Else and P.C. Lee), Cambridge University Press, Cambridge. Pp 329-341.

Caughley, G. (1975): Analysis of Vertebrate Populations. Wiley, Chichester.

Drickamer, L.C. (1974): A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatologica 21*: 61-80.

Dunbar, R.I.M. (1980): Determinants and evolutionary consequences of dominance among female gelada baboons. *Behavioural Ecology and Sociobiology 7*: 253-265.

Fooden, J. (1975): Taxonomy and Evolution of Liontail and Pigtail Macaques (Primates : Cercopithecidae). *Bibliotheca Primatologica* 10. Basel, Karger.

Frisch, R.E. & E. McArthur (1974): Menstrual cycles: fatness as a determinant of minimum weight for the maintenance or onset. *Science 185*: 949-951

Froelich, J.W., Thorington, Jr., & J.S. Otis (1981): The demography of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. *International Journal of Primatology 2*: 207-236.

Keverne, E.B. (1983): Endocrine determinants and constraints on sexual behaviour in monkeys. *In*: Mate Choice, (Ed. P. Bateson). Cambridge University Press, Cambridge, pp. 407-420.

Kumar, A. (1987): The Ecology and Population Dynamics of the Lion-tailed macaque (*Macaca silenus*) in South India. Ph.D. Dissertation submitted to the University of Cambridge, U.K.

Kumar, A. (1995a): The life history, ecology, distribution and conservation problems in the wild. *In*: The Lion-taled Macaque: Population and Habitat Viability Assessment Workshop. Zoo Outreach, Coimbatore, India. Kumar, A., S. Molur and S. Walker (Eds.).

Kumar, A. (1995b): Birth rate and survival in relation to group size in the lion-tailed macaque, *Macaca silenus*. *Primates*, *36*: 1-9.

KUMAR, A. & G.U. KURUP (1985): Sexual behaviour of the Lion-tailed macaque, *Macaca silenus*. *In*: The Lion-tailed Macaque: Status and Conservation (Ed. P.G. Heltne), pp. 109-130, Alan R. Liss, New York.

LINDBURG, D.G. & B.L. LASELY (1985): Strategies of optimising the reproductive potential of lion-tailed macaque colonies in captivity. *In*: The Lion-tailed Macaque: Status and Conservation (Ed. P.G. Heltne), pp. 34-56. Alan R. Liss, New York.

MORI, A. (1979): Analysis of population changes by body weight in the Koshima troop of Japanese monkeys. *Primates* *20*: 371-397.

WASSER, S.K. (1983): Reproductive competition and cooperation among female yellow baboons. *In*: Social Behaviour of Female Vertebrates. (Ed. S.K. Wasser), Academic Press, New York. pp. 349-390.

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